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Tree community patterns along a deciduous to evergreen forest gradient in central Bolivia

Patrones de comunidades de árboles en un gradiente de bosque semideciduo a bosque siempreverde en Bolivia central

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Abstract

We studied trees with a diameter at breast height ≥ 10 cm on three one-hectare plots in the Refugio Los Volcanes seasonal forests (1,000-1,400 m elevation), located in the Andean foothills of central Bolivia. The plots included local variants of deciduous, semi-deciduous and evergreen forest vegetation. We recorded a total of 115 species and 43 families. The most diverse plot was the semi-deciduous forest plot with 70 species, 56 genera and 31 families, whereas the evergreen forest plot had slightly lower richness values (63 species, 49 genera, 31 families). The deciduous forest plot had much lower numbers (44 species, 38 genera and 21 families) and shared only 19 and 15 species with the semi-deciduous and evergreen forest plots, respectively. Between 34% and 50% of the species in the study plots were locally rare species, i.e., species with only one or two individuals per plot. On the other hand, a high percentage of the total number of individuals and basal area was contributed by a few dominant species in each plot. Pachystroma longifolium (Nees) I.M. Johnst. (Euphorbiaceae) was the only species among the three most important species in each of the three plots. Leguminosae was the most important family in the deciduous and semi-deciduous plots. The evergreen forest plot contained different dominant families compared to the other two plots. The species richness values we found in this study were similar to other tree inventories in comparable seasonal forest ecosystems in Bolivia. Species and familial composition, however, were contrastingly different, except for the well-known fact that Leguminosae is the numerically most important family in seasonally dry Neotropical forest ecosystems.Phytogeographically, the tree flora of Los Volcanes is heterogeneous, being composed of elements belonging to seasonal forests as well as to humid tropical forests.
Keywords: Amboró National Park, seasonal forest, tree density, tree dominance, tree inventory.

Resumen

Estudiamos tres parcelas de una hectárea cada una incluyendo todos los árboles con diámetro a la altura del pecho de 10 cm o más en el ecosistema estacional del Refugio Los Volcanes (1.000-

1.400 m de altitud), situado en el centro de Bolivia. Las parcelas incluyeron variantes locales de bosques deciduos, semideciduos y siempreverdes. Encontramos un total de 115 especies y 43 familias. La parcela más diversa fue la semidecidua con 70 especies, 56 géneros y 31 familias; con bosque siempreverde tuvo valores de diversidad similares o ligeramente más bajos (63 especies, 49 géneros, 31 familias); mientras la que presenta bosque deciduo tuvo valores mucho más bajos (44 especies, 38 géneros y 21 familias) y compartía sólo 19 y 15 especies con las parcelas en el bosque semideciduo y siempreverde, respectivamente. Entre un 34% y 50% de las especies en las parcelas eran localmente raras con sólo uno o dos individuos por parcela. Por otro lado, un alto porcentaje del número total de individuos y del área basal era contribuido por unas pocas especies dominantes en cada parcela. "*Pachystroma longifolium* (Nees) I.M. Johnst. (Euphorbiaceae) fue la única especie que estaba entre las tres especies más dominantes en cada una de las tres parcelas. Leguminosae fue la familia más importante en las parcelas de bosque deciduo y semideciduo. El bosque siempreverde contenía un conjunto de familias dominantes distintas a las otras parcelas. Los valores de riqueza de especies fueron similares a otros estudios de inventarios forestales en ecosistemas estacionales comparables realizados en Bolivia. La composición de especies y familias por otro lado, fue diferente, exceptuando el hecho bien conocido que Leguminosae es la familia dominante en bosques estacionalmente secos del Neotrópico. Fitogeográficamente, la flora arbórea de las parcelas de Los Volcanes es heterogénea, estando compuesta de elementos de bosques estacionalmente secos así como de los bosques tropicales húmedos.
Palabras clave: Amboró, Bosque estacional, Densidad de árboles, Dominancia de árboles, Inventario forestal.

Introduction

The Amboró National Park located in the Santa Cruz department (Bolivia) must be one of the most biodiverse protected areas in the world with vegetation types such as lowland humid evergreen forests, inter-Andean dry forests, high altitude cloud forests and puna vegetation from which more than 3,000 plant species have been reported to date (Nee 2004). The southeastern part of the national park is mainly composed of deciduous vegetation and previous classifications have tended to include it in single broad categories. Navarro *et al.* (1996) for example, included this area in the 'subhumid to humid deciduous forest of southeastern Amboró', a vegetation type usually found between 900-1,100 m and where the dominant tree species are *Aspidosperma cylindrocarpum* (Apocynaceae), *Cariniana estrellensis* (Lecythidaceae), *Cedrela lilloi* (Meliaceae), *Gallesia integrifolia* (Phytolaccaceae), *Pachystroma longifolium* (Euphorbiaceae), *Pogonopus tubulosus* (Rubiaceae), and *Tabebuia lapacho* (Bignoniaceae). More recently, Navarro & Maldonado (2002) assigned the vegetation in this area to the 'upper central subandean Cerrado semideciduous forest', found between 1,000-1,900 m and with *P. longifolium* and C. estrellensis dominating the 1,000-1,300 m range. Based on visual inspections of the area, however, we observed substantial variations of the vegetation within these broad categories. During a multidisciplinary study on the ecology of animals and plants at the Refugio Los Volcanes (hereafter LV, an area adjacent to the south of Amboró National Park), we observed that the dominant zonal vegetation in the area was indeed semi-deciduous forest (about 30-50% deciduous trees), mainly found on the shaded south-facing slopes. Local differences in topography and aspect, however, seemed to lead to ecologically relevant differences in water availability. Consequently, steep, sunny and north-facing

slopes were occupied by deciduous forest (70-90% deciduous), whereas the flat, shaded valleys with groundwater supply supported evergreen forest (10-20% deciduous). In order to test these visual observations we established three permanent one-hectare plots along the deciduous to evergreen seasonal forests vegetation gradient of LV. Our aims were to characterise the forest types within the LV area, to understand the relationship between these distinct types using quantitative tree inventories and to investigate the wider biogeographic affinities (within Bolivia and beyond) of the LV forest.

Study area

The study was carried out at the Refugio Los Volcanes (1,000-1,400 m altitude) in Santa Cruz, Bolivia. LV is located at about 18°06′ S and 63°36′ W, adjacent to the southern border of Amboró National Park, on the transition from the humid inner tropics to the seasonally dry subtropics (Fig. 1). The geological substrate of the study area consists primarily of red sandstone and locally of loamy sedimentary rocks (lutite). Annual precipitation is about 1,200-1,400 mm, with a three month dry season from July to October. The deciduous forest plot (18° 06′ 48′′S, 63° 36′ 10′′W) was located at an average altitude of 1,150 m on a sunny north-facing slope. The semi-deciduous forest plot (18° 06′ 13′′S, 63° 35′ 44′′W, 1,300 m northeast of the deciduous forest plot) was located at an average altitude of 1,070 m on a south-facing slope shaded by a rock-wall toward the southeast. The evergreen forest plot (18° 06′ 03′′S, 63° 35′ 58′′W, 500 m northwest of the semi-deciduous forest plot) was located at an average altitude of 1,100 m in a ravine with loose soils and permanent groundwater supply provided by a small watercourse that divided the plot into two parts with steep slopes on both sides of the creek.

Methods

We established one permanent plot of 1 ha in each forest type in 2002-2003. We subdivided each plot into 25 adjacent 20 m x 20 m subplots, which where laid out in such a way as to include only a homogeneous representation of the forest type under study (i.e., avoiding secondary vegetation or other forest types). Thus, our plots are not the traditional square 100 m x 100 m inventory plots, but have rather irregular shapes (Fig. 1). We recorded diameter at breast height (dbh) for each tree with a diameter of 10 cm or more. "Voucher specimens of all species were collected for later taxonomic determination and are deposited at USZ (Santa Cruz) and LPB (La Paz) (herbarium acronyms following Holmgren & Holmgren 1998). Identification of the most common species was done directly in the field whenever possible. Vouchered specimens were identified at USZ and LPB using local (e.g. Jardim *et al.* 2003) and national tree floras (Killeen *et al.* 1993), as well as by comparison with reference collections and expert identification from local and visiting botanists at the mentioned herbaria. Sterile specimens that could not be completely identified were sorted into morphospecies.

We calculated relative density, relative dominance (using basal area) and relative frequency for each species in order to estimate the importance value index (IVI) following Curtis & McIntosh (1951). To calculate the family value index (FVI) we followed Mori *et al.* (1983) and used relative density, relative dominance and relative diversity (number of species per family). We constructed smoothed individual based species accumulation curves by randomly adding individuals to the species accumulation curve. This procedure was repeated 100 times and we used the mean and 1.96 standard deviations to plot the curve and 95% confidence intervals (Magurran 2004).

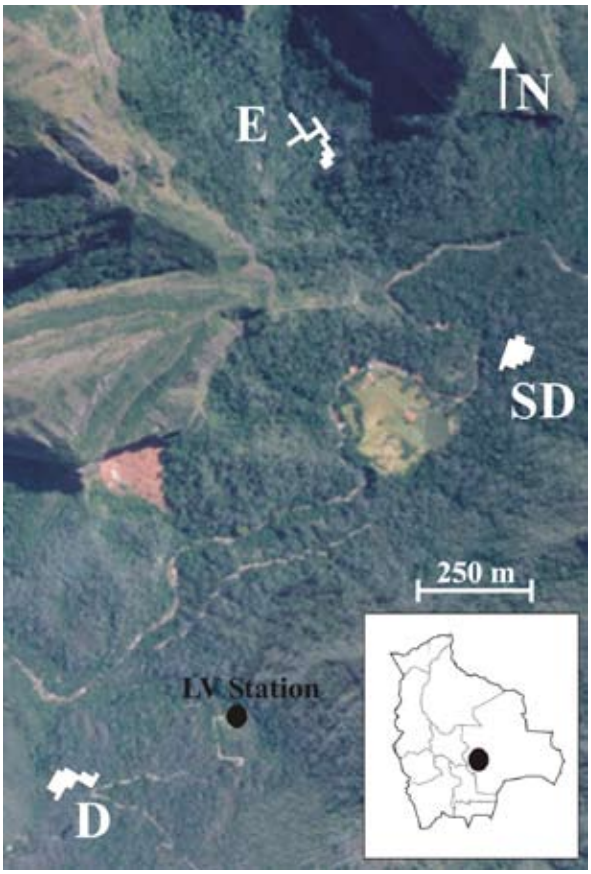

Figure 1. Study area in Refugio Los Volcanes, Santa Cruz (inset shows location within Bolivia). Plot shape and approximate location are given by D (deciduous forest), SD (semi deciduous forest) and E (evergreen forest).

Results

Diversity and density

We recorded 115 tree species from 43 families on the three 1-ha plots (Appendix 1). The semi-deciduous and evergreen forest plots were the most species-rich (Table 1). In contrast, density values were much higher on the deciduous forest plot, where multi-stemmed trees were about twice as common as on the other two plots. A higher percentage of species represented by a single individual (singleton) and by two individuals (doubletons) was found in the semi-deciduous and evergreen forest plots (Table 1). Overall, locally rare species represented by one or two individuals accounted for 34-50% of the species on our study plots.

We found no lianas or hemi-epiphytes with a dbh ≥10 cm on the deciduous forest plot. The semi-deciduous forest plot contained five individuals of hemi-epiphytes (*Ficus* sp., *F. obtusifolia* Kunth in Humb., Bonpl. & Kunth and *F. trigona* L. f., Moraceae) and two of lianas (*Machaerium* cf. *punctatum* (Poir.) Pers., Leguminosae and *Celtis iguanaea* (Jacq.) Sarg., Ulmaceae). The evergreen

Table 1. General diversity and structural characteristics of three one-hectare plots in central Bolivia.

	Deciduous	Semi-deciduous	Evergreen
Species	44	70	63
Genera	38	56	49
Families	21	31	31
# Individuals	640	572	537
# stems	706	612	569
% multistemmed trees	9.5%	4.9%	5.6%
Singletons	10 (23%)	24 (34%)	20 (32%)
Doubletons	5 (11%)	11 (16%)	10 (16%)

forest plot contained eight individuals of hemi-epiphytes (*Ficus* cf. *eximia* Schott in Spreng., *F. maxima* Mill., *F. obtusifolia* Kunth in Humb., Bonpl. & Kunth, *F. pertusa* L. f. and *F. trigona* L. f., Moraceae) and no lianas.

Individual based species accumulation curves showed that when up to ca. 180 individuals are sampled randomly from each plot, confidence intervals of the estimated species richness values overlap, indicating that the observed differences could have arisen by chance (Fig. 2). Increased random sampling of individuals, however, revealed clear differences between the deciduous forest plot and the two other forest plots. Nevertheless, irrespective of increased sampling these two latter forest types showed very similar estimated species richness values up to the total individuals sampled.

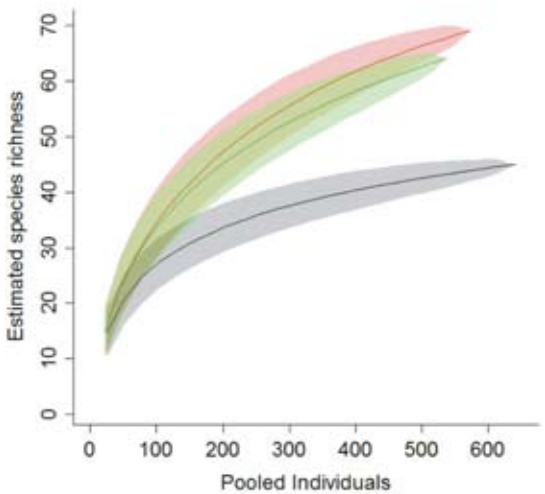

Figure 2. Individual based species accumulation curves of the deciduous (black), semi-deciduous (red) and evergreen (green) forest plots. Lines indicate estimated species richness values by given number of individuals; polygons indicate a 95% confidence interval.

Diameter distribution in size classes

The range of dbh values increased from the deciduous forest plot (10-83 cm) to the evergreen forest plot (10-162 cm), with intermediate values on the semi-deciduous forest plot (10-125 cm). Basal area was highest on the semi-deciduous and deciduous forest plots with 27.7 m^2 and 27.5 m^2, respectively. The evergreen forest plot had a somewhat lower basal area with 24.2 m^2. All three plots showed a left-skewed "inverted J" distribution of the number of individuals per dbh size class (Fig. 3). Nevertheless, there were differences in the dbh size class that contributed most to total basal area (Fig. 3). Dbh size classes from 10-50 cm contributed most on the deciduous forest plot (with 11.4 to 14.9% of total basal area per size class). On the semi-deciduous forest plot, the 30-40 cm dbh size class contributed with 22.6% of total basal area. On the evergreen forest plot low dbh size classes, as well as high dbh classes, were responsible for most of the total basal area (dbh size classes 10-15 cm and 15-20 cm contributed with 12.1% and 11.4% of total basal area, respectively. The dbh size class of 100 cm or more contributed with 13.1%).

Dominant species and families

The deciduous forest plot (Table 2) was dominated by *Parapiptadenia excelsa* (Griseb.) Burkart (Leguminosae) and *Trichilia claussenii* C. DC. (Meliaceae). Both had the highest number of individuals (97 and 98, respectively) and together contributed to more than 30% of the total number of individuals on the plots and to 24% of total basal area (8% and 16%, respectively). Other important and dominant species were *Aspidosperma cylindrocarpon* Mull. Arg. (Apocynaceae), *Schinopsis hankeana* Engl. (Anacardiaceae), *Pachystroma longifolium* (Nees) I.M. Johnst. (Euphorbiaceae), and *Anadenanthera colubrina* (Vell.) Brenan (Leguminosae). They contributed with 24% of the total number of individuals and 41% of total basal area. Together these six species represented the 54% of all individuals and 62% of total basal area. The most important family was Leguminosae with 32% of the individuals, 12 species and 39% of the basal area, followed by Meliaceae and Euphorbiaceae. These three families contributed with 58% of the number of individuals, 54% of basal area and 40% of species richness (Table 2).

The semi-deciduous forest plot (Table 3) was dominated by *Pachystroma longifolium* and *Myrciantes* cf. *pseudomato* (Legrand) Mc. Vough. (Myrtaceae). *Pachystroma longifolium* had the highest number of individuals (118, 21% of the total), and both species had the highest basal area, comprising 38% of total basal area. Other important species in terms of density were *Chomelia* cf. *sessilis* Mull. Arg. (Rubiaceae) and *Chrysophyllum gonocarpum* (Mart. & Gichl.) Engl. (Sapotaceae). The most important family was Euphorbiaceae, in which only two species contributed 25% of the individuals and 21% of basal area, followed by Sapotaceae and Myrtaceae. These three families comprised 47% of the number of individuals, 55% of basal area and 13% of species richness (Table 4).

The evergreen forest plot (Table 5) was dominated by *Aniba* sp. (Lauraceae), with 76 individuals (14% of the total) and 8% of total basal area. *Drypetes amazonica* Steyerm. (Euphorbiaceae), *Pachystroma longifolium* and *Clarisia biflora* Ruiz & Pav. (Moraceae) were also important. These four species contributed 40% of the total number of individuals and 26% of total basal area. The most important family was Moraceae with 74 individuals (14% of the total), 25% of total basal area and eight species, followed by Lauraceae, Sapotaceae and Euphorbiaceae. These four families represented 66% of the individuals, 70% of basal area and 35% of species richness (Table 6).

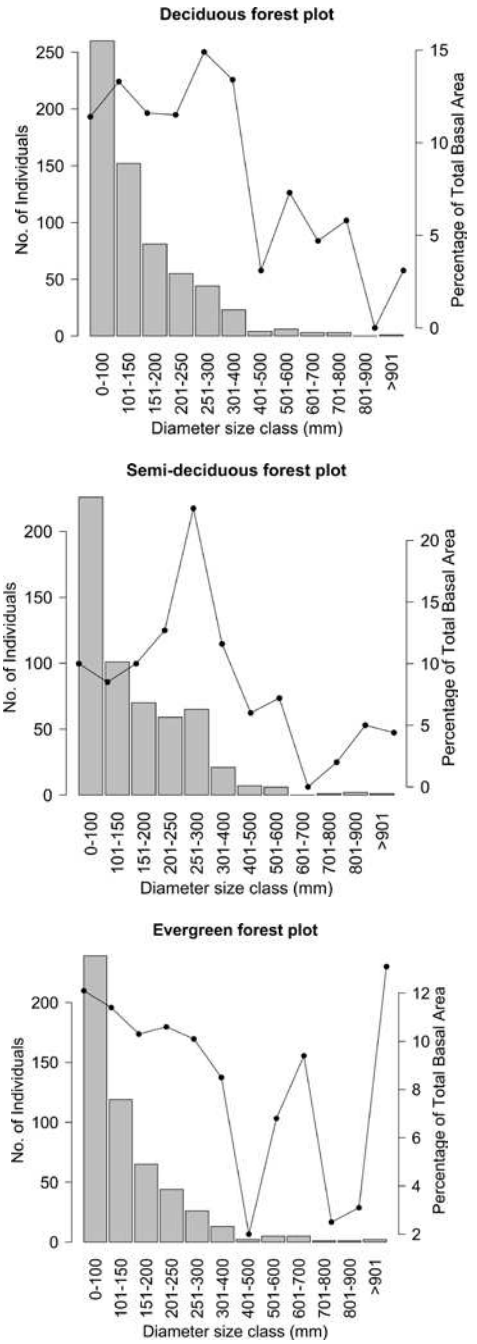

Figure 3. Number of individuals (bars) and percentage contribution of total basal area (lines) per diameter size class on three 1-hectare forest plots in central Bolivia. Note different scales of the ordinates for each graph.

Table 2. Ten most dominant woody plants with dbh ≥10cm in the deciduous forest plot according to importance value indices (species are ranked by descending importance value index). Legend: # Ind = no. of individuals, rDe = relative density, BA = basal area, rDo = relative dominance, F = frequency, rF = relative frequency, IVI = importance value indices.

Family	Species	# Ind	rDe	BA	rDo	F	rF	IVI
LEG	*Parapiptadenia excelsa* (Griseb.) Burkart	97	15.16	3.71	13.48	20	7.33	35.96
MEL	*Trichilia claussenii* C. DC.	98	15.31	2.13	7.73	19	6.96	30.01
APO	*Aspidosperma cylindrocarpon* Mull. Arg.	43	6.72	2.55	9.27	17	6.23	22.22
ANA	*Schinopsis hankeana* Engl.	17	2.66	4.30	15.63	10	3.66	21.95
EUP	*Pachystroma longifolium* (Nees) I.M.	57	8.91	1.99	7.23	15	5.49	21.63
LEG	*Anadenanthera colubrina* (Vell.) Brenan	35	5.47	2.39	8.69	12	4.40	18.56
NYC	*Neea* sp.	30	4.69	0.70	2.53	15	5.49	12.71
URT	*Pouzolzia* sp.	32	5.00	0.46	1.66	15	5.49	12.16
LEG	*Tipuana tipu* (Benth.) Kuntze	11	1.72	1.98	7.19	5	1.83	10.74
LEG	*Piptadenia buchtienii* Barneby	21	3.28	0.84	3.05	12	4.40	10.73

Table 3. Ten most dominant families of woody plants with dbh ≥10cm in the deciduous forest plot according to family value indices (families are ranked by descending family importance value). Legend: # Ind = no. of individuals, rDe = relative density, BA = basal area, rDo = relative dominance, Div = species diversity, rDiv = relative diversity, FIV = family importance value.

Family	# Ind	rDe	BA	rDo	Div	rDiv	FIV
Leguminosae	208	32.50	10.70	38.89	12	27.27	98.66
Meliaceae	99	15.47	2.28	8.29	2	4.55	28.30
Euphorbiaceae	66	10.31	2.12	7.71	4	9.09	27.11
Anacardiaceae	23	3.59	4.48	16.28	2	4.55	24.42
Apocynaceae	47	7.34	2.63	9.56	2	4.55	21.45
Nyctaginaceae	33	5.16	0.78	2.83	3	6.82	14.81
Capparidaceae	26	4.06	0.67	2.44	2	4.55	11.04
Sapotaceae	25	3.91	0.42	1.53	2	4.55	9.98
Urticaceae	32	5.00	0.46	1.67	1	2.27	8.94
Myrtaceae	5	0.78	0.10	0.36	3	6.82	7.96

Table 4. Ten most dominant woody plants with dbh ≥10cm in the semi-deciduous forest plot according to importance value indices (species are ranked by descending importance value index). Legend: # Ind = no. of individuals, rDe = relative density, BA = basal area, rDo = relative dominance, F = frequency, rF = relative frequency, IVI = importance value indices.

Family	Species	# Ind	rDe	BA	rDo	F	rF	IVI
EUP	*Pachystroma longifolium* (Nees) I.M. Johnst.	118	20.59	5.43	19.63	23	7.42	47.64
MYRT	*Myrciantes* cf. *pseudomato* (Legrand) Mc. Vough.	38	6.63	5.01	18.11	17	5.48	30.23
RUB	*Chomelia* cf. *sessilis* Mull. Arg.	40	6.98	2.11	7.63	15	4.84	19.45
SAPO	*Chrysophyllum gonocarpum* (Mart. & Gichl.) Engl.	32	5.58	1.61	5.82	17	5.48	16.89
SAPO	*Sarcaulus* sp.	35	6.11	0.44	1.59	15	4.84	12.54
EUP	*Drypetes amazonica* Steyerm.	28	4.89	0.48	1.74	16	5.16	11.78
APO	*Aspidosperma rigidum* Rusby	25	4.36	0.48	1.74	12	3.87	9.97
MOR	*Sorocea guilleminiana* Gaudich.	22	3.84	0.23	0.83	16	5.16	9.83
SAPO	*Chrysophyllum venezuelanense* (Pierre) T.D. Penn.	11	1.92	1.29	4.66	8	2.58	9.16
PHY	*Gallesia integrifolia* (Sprengel) Harms	6	1.05	1.74	6.29	5	1.61	8.95

Table 5. Ten most dominant families of woody plants with dbh ≥10cm in the semi-deciduous forest plot according to family value indices (families are ranked by descending family importance value). Legend: # Ind = no. of individuals, rDe = relative density, BA = basal area, rDo = relative dom inance, Div = species diversity, rDiv = relative diversity, FIV = family importance value.

Family	# Ind	rDe	BA	rDo	Div	rDiv	FIV
Euphorbiaceae	146	25.48	5.91	21.37	2	2.50	49.35
Sapotaceae	80	13.96	4.08	14.75	4	5.00	33.71
Myrtaceae	42	7.33	5.15	18.62	3	3.75	29.70
Leguminosae	33	5.76	1.66	6.00	9	11.25	23.01
Rubiaceae	46	8.03	2.2	7.95	3	3.75	19.73
Lauraceae	38	6.63	0.98	3.54	6	8.75	18.92
Apocynaceae	49	8.55	1.43	5.17	4	5.00	18.72
Moraceae	35	6.11	0.69	2.49	6	7.50	16.10
Tiliaceae	3	0.52	0.12	0.43	11	13.75	14.71
Meliaceae	22	3.84	0.36	1.30	4	5.00	10.14

Discussion

Effect of plot shape on species richness and community composition estimations

Spatial distribution patterns of plant species in tropical forests have been reported to show mostly clumped distributions (e.g., Condit *et al.* 2000). Within this scenario, longer and narrower rectangular plots are prone to capture more species than square plots of similar area, because the former could include a potentially more heterogeneous area (Condit *et al.* 1996, Laurance *et al.* 1998). Nevertheless, small and statistically non-significant differences were found in a study comparing tree diversity in square plots versus rectangular plots in Central Amazonia (Laurance *et al.* 1998). Given the patchy and fragmented nature of the deciduous and evergreen forests in our study area, it was impossible to survey all vegetation types in regular square or rectangular plots. Rather, we tried to survey as environmentally homogeneous an area as possible, leading to our irregular plot shape design. We acknowledge that plot shape has influenced our results, especially those of the transect-like evergreen forest plot. The extent of this influence, however, seems to be variable, as can be seen from the species accumulation curves. It significantly decreased in the irregularly shaped deciduous forest plot when the hectare was completely surveyed, suggesting that sampling was representative. In contrast, the species accumulation curves did not level off in the more-or-less regularly shaped semi-deciduous plot and in the long and transect-like evergreen forest plot, suggesting, that sampling, irrespective of plot shape, was incomplete.

Table 6. Ten most dominant woody plants with dbh ≥10cm in the evergreen forest plot according to importance value indices (species are ranked by descending importance value index). Legend: # Ind = no. of individuals, rDe = relative density, BA = basal area, rDo = relative dominance, F = frequency, rF = relative frequency, IVI = importance value indices.

Family	Species	# Ind	rDe	BA	rDo	F	rF	IVI
LAU	*Aniba* sp.	76	14.18	1.95	8.05	23	7.42	29.65
EUP	*Drypetes amazonica* Steyerm.	60	11.19	0.91	3.76	22	7.10	22.05
EUP	*Pachystroma longifolium* (Nees) I.M. Johnst.	43	8.02	1.81	7.47	17	5.48	20.98
MOR	*Clarisia biflora* Ruiz & Pav.	38	7.09	1.53	6.31	19	6.13	19.53
SAPO	*Pouteria nemorosa* Baehni	11	2.05	2.64	10.90	10	3.23	16.17
URT	*Myriocarpa stipitata* Benth.	35	6.53	0.78	3.22	10	3.23	12.97
SAPO	*Chrysophyllum gonocarpum* (Mart. & Gichl.) Engl.	21	3.92	0.69	2.85	14	4.52	11.28
MOR	*Ficus* cf. *eximia* Schott in Spreng.	3	0.56	2.26	9.33	3	0.97	10.85
NYC	*Guapira* aff. *olfersiana* (Link et al) Standl.	17	3.17	0.79	3.26	11	3.55	9.98
MOR	*Sorocea guilleminiana* Gaudich.	22	4.10	0.25	1.03	15	4.84	9.97

Table 7. Ten most dominant families of woody plants with dbh ≥10cm in the evergreen forest plot according to family value indices (families are ranked by descending family importance value). Legend: # Ind = no. of individuals, rDe = relative density, BA = basal area, rDo = relative dominance, Div = species diversity, rDiv = relative diversity, FIV = family importance value.

Family	# Ind	rDe	BA	rDo	Div	rDiv	FIV
Moraceae	74	13.81	6.04	24.93	8	12.90	51.64
Lauraceae	118	22.01	3.21	13.25	6	9.68	44.94
Sapotaceae	56	10.45	4.69	19.36	5	8.06	37.87
Euphorbiaceae	104	19.40	2.87	11.84	3	4.84	36.09
Urticaceae	40	7.46	0.88	3.63	2	3.23	14.32
Leguminosae	7	1.31	0.63	2.60	4	6.45	10.36
Rubiaceae	12	2.24	0.58	2.39	3	4.84	9.47
Araliaceae	13	2.43	0.7	2.89	2	3.23	8.54
Meliaceae	16	2.99	0.17	0.70	3	4.84	8.53
Apocynaceae	15	2.80	0.6	2.48	2	3.23	8.50

Local variation of tree diversity, dominance and structure at Los Volcanes

There were obvious differences in the diversity and floristic composition between the deciduous forest plot and the two other plots, which where rather similar in diversity and structure. Not only was the deciduous forest plot poorer in terms of generic and familial diversity, it also shared fewer species with the semi-deciduous and the evergreen forest plot. The deciduous forest plot shared 19 species with the semi-deciduous and 15 with the evergreen forest plot, whereas the latter two shared 39 species. Eleven species were present in all three plots and represented a selection of the tree species characteristic of the Amboró region like *Aspidosperma cylindrocarpum*, *Gallesia integrifolia* and *Pachystroma longifolium* (Navarro *et al.* 1996). Few of these species were dominant and abundant on each of the plots, such as *Chrysophyllum gonocarpum*. On the contrary, most were locally rare species, at least at the hectare-scale, with abundances of one individual per hectare (e.g., *Cariniana estrellensis* (Raddi) Kuntze, *Swartzia jorori* Harms, *Eugenia* sp.).

Differences in diversity and composition between the three plots, especially between the deciduous forest plot and the two other, was mirrored by several environmental factors. For example, soil humidity and pH increased from the deciduous forest plot to the evergreen forest plot (Lendzion 2003). Therefore, even though there is a dominant regional flora, small-scale environmental variations produce significant differences in the composition and dominance of the local tree flora. This fact has already been shown for terrestrial herbs at LV (Lendzion 2003) and for woody species in seasonal forests elsewhere (Oliveira-Filho *et al.* 1998, Balvanera *et al.* 2002).

Lianas have been considered important components of tropical forests (Medina 1995), constituting in some cases 20% or more of the local flora (Gentry 1995, Schnitzer & Bongers 2002). In this study, however, we were not able to record lianas with a dbh ≥ 10 cm in the

deciduous and evergreen forest plots. Only the semi-deciduous forest plot contained two individuals belonging to two tree species (*Machaerium* cf. *punctatum* and *Celtis iguanaea*), which occasionally also grow as lianas, with a dbh ≥10 cm. This agrees with another study in Bolivian deciduous forests that found similar low levels of liana diversity and density using the same sampling methodology (Cayola *et al.* 2005). Nonetheless, this does not mean that the LV forests are devoid of vines and climbers. In fact, most of the liana diversity and abundance in each of the studied forest plots is found in dbh classes below 10 cm (Hoffmann 2004), so that our results have to be interpreted as a sampling artefact.

In mountainous areas, with forest growing on steep slopes, one of the factors than can influence and produce low basal area values are landslides (Chazdon 2003). Since the humid forest plot was located on steeper slopes than the other two plots and additionally had rather loose soils, we suggest that an increased frequency of localized landslides could have produced the lower basal area as compared to the other two plots.

The Los Volcanes forests in a Bolivian context

Our inventory on the deciduous forest plot contained species richness and densities of trees with dbh ≥ 10 cm within the range of other inventories in Bolivian seasonal forests (Table 8). It was much richer and denser than that of the Santa Cruz Botanical Garden (inventoried by Uslar *et al.* 2004), which is located in a slightly drier lowland area (350 m). Our plots in the semi-deciduous and evergreen forest variants, although much more species-rich, were less dense than the San Rafael (1,500 m, Vargas 1995) and Río Tuichi (880 m, Cayola *et al.* 2005) plots.

The dominant and most diverse family in seasonal deciduous forests in the Neotropics is usually Leguminosae (Gentry 1995, Pennington *et al.* 2006). There is, however, ample variation as to which are the next most diverse and dominant families. This is confirmed by several other inventories in Bolivian deciduous forests (Killeen *et al.* 1998, Kessler & Helme 1999, Fuentes Claros *et al.* 2004) and by our study, where we had six different families following Leguminosae in importance. In nearby Santa Cruz (Uslar *et al.* 2004) Leguminosae was the dominant family (seven species), all other families with only one or two species (Table 8). In the adjacent Amboró National Park (Vargas 1995), they were Lauraceae and Myrtaceae. Finally, the Tuichi valley dry forests inventory in La Paz department (Cayola *et al.* 2005) reported also Myrtaceae and Bombacaceae as important. The dominant families on the evergreen forest plot in LV showed contrasting results with Moraceae, Lauraceae and Sapotaceae as the most diverse families (Table 8). The diversity of Moraceae, whose members are prominent components of tropical rain forests, already suggests the prevalence of different local environmental conditions on this plot.

In contrast, species composition and densities of trees with dbh ≥ 10 cm on the LV plots differed from other tree inventories in Bolivia with similar annual rainfall and similar seasonal vegetation. For instance, the Santa Cruz plot in the deciduous Chiquitania forests (Uslar *et al.* 2004) reported *Aspidospermum cylindrocarpon* (Apocynaceae), *Myrciaria cauliflora* (Myrtaceae) and *Phyllostylon rhamnoides* (Ulmaceae) as the most abundant species (Table 8). The Rio San Rafael plot in Amboró contained *Nectandra* sp. (Lauraceae), *Casearia* sp. (Flacourtiaceae) and *Chrysophyllum* cf. *gonocarpum* (Sapotaceae) as the most frequent species (Vargas 1995). The three most common species in the Tuichi plot were *Phyllostylon rhamnoides* (Ulmaceae), *Trichilia catigua* (Meliaceae) and *Anadenanthera colubrina* (Leguminosae) (Cayola *et al.* 2005). At LV, the most abundant species were *Trichilia claussenii*, *Parapiptadenia excelsa* and *Pachystroma longifolium* on the deciduous forest plot, *Pachystroma longifolium*, *Chomelia* cf. *sessilis*

Table 8. Seasonal forest inventories in Bolivia with diameter cut-off of 10 cm. Legend: Ind = No. of individuals, BA = basal area, Alt. = altitude, dry s. = length of the dry season, NA = data not available.

Plot (Reference)	Species	3 most dense species	Families	3 most diverse families	Ind.	BA (m^2)	Plot shape	Alt. (m)	Rainfall (mm/ year)	dry s. (months)
Jardin Botánico Santa Cruz (Uslar *et al.* 2004)	28	*Aspidospermum cylindrocarpon* (99) *Myrciaria cauliflora* (91) *Phyllostylon rhamnoides* (79)	18	Leguminosae	503	27	100x100	375	1.122	6
Rio San Rafael (Vargas 1995)	50	*Nectandra* sp. (158) *Casearia* sp. (117) *Chrysophyllum* cf. *gonocarpum* (74)	33	Lauraceae (6), Leguminosae (4), Myrtaceae (3)	713	27.7	irregular	1.500	1.500	NA
Tuichi (Cayola *et al.* 2005)	51	*Phyllostylon rhamnoides* (197) *Trichilia catigua* (96) *Anadenanthera colubrina* (48)	24	Leguminosae (10), Myrtaceae (4), Bombacaceae, Cactaceae, Flacourtiaceae, Meliaceae, Polygonaceae (3)	697	20	NA	880	1.300	3
LV Deciduous (This study)	44	*Trichilia claussenii* (98) *Parapiptadenia excelsa* (97) *Pachystroma longifolium* (57)	21	Leguminosae (12), Euphorbiaceae (4), Nyctaginaceae and Myrtaceae (3)	640	27.5	irregular	1.055	1.600	3
LV Semi-deciduous (This study)	70	*Pachystroma longifolium* (118) *Chomelia* cf. *sessilis* (40) *Myrciantes cf.* pseudo-mato (38)	32	Leguminosae (9), Lauraceae (6), Moraceae (6)	572	27.7	irregular	1.073	1.600	3
LV Evergreen (This study)	63	*Aniba* sp. (76) *Drypetes amazonica* (60) *Pachystroma longifolium* (43)	31	Moraceae (8), Lauraceae (6), Sapotaceae (5)	537	24.2	irregular	1.104	1.600	3

and *Myrciantes* cf. *pseudo-mato* on the semi-deciduous forest plot, and *Aniba* sp., *Drypetes amazonica* and *Pachystroma longifolium* on the evergreen forest plot (Table 8).

In terms of basal area, our deciduous and semi-deciduous forest inventories reached similar values of around 27 m^2, which is comparable to other seasonal forest inventories in Bolivia, except for the Tuichi plot in La Paz (20 m^2) and our evergreen forest plot in LV (24.2 m^2). Murphy & Lugo (1986) stated that seasonal forests were less complex structurally than wet tropical forests, with basal area values in the range from 17 m^2 to 40 m^2. Several other studies have reaffirmed this statement (e.g., Lopes *et al.* 2008). Basal area values of the LV plots, however, were also within the range of other tree inventories in several vegetation types in South America, using the same diameter cut-off, and particularly within Bolivia. For instance, basal area values of several 1-ha inventories in humid tropical forests ranged between 21.4 m^2 (Beni, Bolivia) and 39.2 m^2 (Amboró, Bolivia) (Smith & Killeen 1998).

Phytogeography of the Los Volcanes species

Based on the distribution of over 70 plant taxa, Prado & Gibbs (1993) proposed the existence of a Pleistocenic arc of seasonal forest formations. The extant fragments of this arc are mainly located in three nuclei: the Caatinga nucleus in northeastern Brazil; the Misiones nucleus comprising the area from the Bolivia-Brazil border in Corumbá southwards to the Paraguay-Paraná river confluence and eastward to Santa Catarina in Brazil; and the piedmont nucleus extending from Santa Cruz de la Sierra in Bolivia southward to Tucumán and the sierras of Catamarca in Argentina. Because our study area is located within the area of the piedmont nucleus (cf. Prado 2000), we examined the distribution patterns of the 115 species found at LV. We recorded *Anadenanthera colubrina*, *Myracrodruon urundeuva* Allemao and *Celtis iguanaea* in our plots, all of which have been reported as characteristic to the wider Pleistocenic arc formation (Prado & Gibbs 1993). We also found *Diatenopteryx sorbifolia* Radlk., classified as a restricted Arc species since it only occurs in the Misiones and Piedmont nuclei. Navarro & Maldonado (2002), who considered the area around LV as transitional between the Brasilian-Parana biogeographic region and the Bolivian-Tucuman biogeographic province, also noted this affinity with the seasonal vegetation in the Misiones and piedmont nuclei. In total, we identified 21 species as typical of Bolivian seasonal forest formations. More complex and widespread distribution patterns are attributed to *Cordia alliodora* (Ruiz & Pav.) Cham. and *Ximenia americana* L., the later occurring in diverse vegetation types throughout the Neotropics.

On a local scale, the forests at LV shared only 21% (24 species) of all recorded tree species with the inventories in Santa Cruz, San Rafael and Tuichi. As expected, the deciduous forest plot shared most species (10 species, 23%) with the nearby (65 km) deciduous forests in the Santa Cruz Botanical Garden and less than 12% with the other two inventories (43 km to San Rafael, 660 km to Tuichi). In contrast, the semi-deciduous forest plot shared only 13% of its species with the inventory in the Santa Cruz Botanical Garden, and less than 10% of its species were also present in the other two inventories. The evergreen forest shared even fewer species with any of the other seasonal forest inventories (less than 11%). Low percentages of shared species between seasonal forest inventories, irrespective of geographical distance, have also been reported for the seasonally dry forest in Mexico and attributed to the existence of processes of high local diversification, possibly due to particular historical processes (Trejo & Dirzo 2002). Indeed, the complex vegetational arrangement of the area - a region where four major biomes

come into contact: the humid vegetation from Amazonia, the seasonal subtropical lowland vegetation from the Chaco, the subtropical highland vegetation from the Andes and the seasonal vegetation of the Chiquitanía (Ibisch *et al.* 2003) - would have provided an optimal setting for the extraordinary floristic diversification in the Santa Cruz region. Thus, even though we are comparing seasonal forest with similar rainfall, dry season length or at similar altitude, their low floristic similarity seems to be strongly influenced by the biome they are closest to. The San Rafael plot in Amboró National Park will be more likely influenced by the Andean biome, the Tuichi plot by the northern Bolivian Andes and Amazonia and Santa Cruz Botanical Garden by the Chiquitania and the Chaco. In similar fashion, the different vegetation types reported at LV have probably been influenced by all these major biomes, and it is the varied local environmental characteristics that have allowed the co-existence of species with differing ecological requirements.

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Appendix 1. Presence-absence data of the tree species with diameter at breast height ≥ 10 cm classified as a restricted Arc species since it only occurs in the Misiones and Piedmont nuclei. Legend: DF = deciduous forest plot, SDF = semi-deciduous forest plot, EF = evergreen forest plot.

Family	Species	DF	SDF	EF
ACT	*Saurauria peruviana* Buscal.			x
ANA	*Myracrodruon urundeuva* Allemao	x		
ANA	*Schinopsis hankeana* Engl.	x		
ANA	*Tapirira* cf. *guianensis* Aubl.		x	
ANN	*Guatteria alutacea* Diels var. *steinbachii* R. E. Fries		x	x
ANN	*Rollinia* sp.1			x
APO	*Aspidosperma cylindrocarpon* Mull. Arg.	x	x	x
APO	*Aspidosperma rigidum* Rusby	x	x	x
APO	*Tabernaemontana cymosa* Jacq.		x	
ARA	*Aralia soratensis* March.		x	
ARA	*Dendropanax arboreus* (L.) Decne. & Planch.		x	x
ARA	*Oreopanax* cf. *steinbachianus* Harms			x
BIG	*Tabebuia heptaphylla* (Vell.) Toledo	x	x	
BOM	*Ceiba boliviana* Britton & Baker f.	x	x	
BOR	*Cordia alliodora* (Ruiz & Pav.) Cham.	x	x	
CAP	*Capparis flexuosa* (L.) L.	x		
CAP	*Capparis prisca* Macbr.	x		
CEC	*Cecropia* sp.		x	x
CEL	*Schaefferia argentinensis* Speg.			x
CHR	*Couepia* sp.		x	
EUP	*Alchornea glandulosa* Poepp.			x
EUP	*Croton piluliferus* Rusby	x		
EUP	*Drypetes amazonica* Steyerm.	x	x	x
EUP	*Pachystroma longifolium* (Nees) I.M. Johnst.	x	x	x
EUP	*Sebastiania brasiliensis* Spreng.	x		
FLA	*Casearia gossypiosperma* Briq.	x		x
FLA	*Casearia* sp.1		x	
FLA	*Casearia* sp.2		x	
FLA	*Hasseltia floribunda* Kunth		x	x
JUG	*Juglans australis* Griseb.			x
LAC	*Lacistema* cf. *aggregatum* (P.J. Bergius) Rusby			x
LAU	*Aniba* sp.		x	x
LAU	Lauraceae 1		x	
LAU	Lauraceae 2		x	
LAU	*Licaria* cf. *triandra* (Sw.) Kosterm.		x	x
LAU	*Nectandra* cf. *cuspidata* Nees & Mart.		x	
LAU	*Nectandra* sp. 1		x	x
LAU	*Nectandra* sp. 2		x	x
LAU	*Nectandra* sp. 3			x

Family	Species	DF	SDF	EF
LAU	*Ocotea* sp.			x
LEC	*Cariniana estrellensis* (Raddi) Kuntze	x	x	x
LEG	*Acacia* cf. *glomerosa* Benth.	x		
LEG	*Acacia* sp. 3	x		
LEG	*Anadenanthera colubrina* (Vell.) Brenan	x		
LEG	*Erythrina falcata* Benth.		x	x
LEG	*Inga marginata* Willd.		x	x
LEG	*Inga* sp. 1		x	x
LEG	*Lonchocarpus hedyosmus* Miq.	x	x	
LEG	*Machaerium* cf. *punctatum* (Poir.) Pers.		x	
LEG	*Machaerium* cf. *scleroxylon* Tul.	x		
LEG	*Machaerium pilosum* Benth.	x		
LEG	*Myroxylon balsamu*n (L.) Harms.	x		
LEG	*Ormosia bolivarensis* C.H. Stirt.		x	
LEG	*Parapiptadenia excelsa* (Griseb.) Burkart	x	x	
LEG	*Piptadenia buchtienii* Barneby	x		
LEG	*Platymiscium* cf. *stipulare* Benth.		x	
LEG	*Senna* sp.	x		
LEG	*Swartzia jorori* Harms	x	x	x
LEG	*Tipuana tipu* (Benth.) Kuntze	x		
MAL	*Bunchosia* cf. *paraguariensis* Nied.	x		x
MEL	*Cedrela lilloi* C. DC.	x	x	
MEL	*Trichilia claussenii* C. DC.	x	x	x
MEL	*Trichilia elegans* A. Juss.		x	x
MEL	*Trichilia pleeana* (A. Juss.) C. DC.		x	x
MELA	*Miconia* cf. *minutiflora* (Bonpl.) DC.			x
MOR	*Clarisia biflora* Ruiz & Pav.		x	x
MOR	*Ficus* cf. *eximia* Schott in Spreng.			x
MOR	*Ficus macbridei* Standl.			x
MOR	*Ficus maxima* Mill.			x
MOR	*Ficus obtusifolia* Kunth in Humb., Bonpl. & Kunth		x	x
MOR	*Ficus pertusa* L. f.			x
MOR	*Ficus* sp.		x	
MOR	*Ficus trigona* L. f.		x	x
MOR	*Maclura tinctoria* (L.) D. Don ex Steud.		x	
MOR	*Sorocea guilleminiana* Gaudich.		x	x
MYRS	*Myrsine umbellata* Mart.		x	x
MYRT	*Eugenia* cf. *moraviana* O. Berg		x	
MYRT	*Eugenia muricata* DC.			x
MYRT	*Eugenia* sp.	x	x	x
MYRT	*Myrciantes* cf. *pseudomato* (Legrand) Mc. Vough.	x	x	
MYRT	*Myrciantes* sp. 1	x		
NYC	*Bougainvillea stipitata* Griseb.	x		
NYC	*Guapira* aff. *olfersiana* (Link et al) Standl.		x	x

Family	Species	DF	SDF	EF
NYC	*Neea* sp.	x		
NYC	Nyctaginaceae Indet	x		
OCH	*Ouratea* cf. *angulata* Tiegh.			x
OLA	*Ximenia americana* L.	x		
PHY	*Gallesia integrifolia* (Sprengel) Harms	x	x	x
PIP	*Piper amalago* L.		x	
POL	*Ruprechtia apetala* Wedd.	x		
POL	*Triplaris americana* L.		x	x
RHA	*Rhamnidium elaeocarpum* Reissek		x	
ROS	*Prunus guanaiensis* Rusby		x	
RUB	*Chomelia* cf. *sessilis* Mull. Arg.		x	x
RUB	*Macrocnemum roseum* (Ruiz & Pav.) Wedd.			x
RUB	*Palicourea* cf. *guianensis* Aubl.			x
RUB	*Pogonopus* sp.		x	
RUB	*Pogonopus tubulosus* (A. Rich.) K. Schum.		x	
SAB	*Meliosma herbertii* Rolfe			x
SAPI	*Allophylus* cf. *edulis* (A. St.-Hil., Cambess. & A. Juss.) Radlk.		x	x
SAPI	*Diatenopteryx sorbifolia* Radlk.	x	x	x
SAPO	*Chrysophyllum gonocarpum* (Mart. & Gichl.) Engl.	x	x	x
SAPO	*Chrysophyllum marginatum* (Hook. & Arn.) Radlk.	x		x
SAPO	*Chrysophyllum venezuelanense* (Pierre) T.D. Penn.		x	x
SAPO	*Pouteria nemorosa* Baehni		x	x
SAPO	*Sarcaulus* sp.		x	x
SIM	*Picrasma excelsa* (Sw.) Planch.		x	
SOL	*Solanum riparium* Pers.		x	
SOL	*Solanum sessile* Ruiz & Pav.			x
TIL	*Heliocarpus americanus* L.		x	x
ULM	*Celtis iguanaea* (Jacq.) Sarg.		x	
URT	*Myriocarpa stipitata* Benth.		x	x
URT	*Pouzolzia* sp.	x	x	
URT	*Urera baccifera* (L.) Gaudich.		x	x
VER	*Aegiphila steinbachii* Moldenke	x		x